

# Underwater behaviour of green turtles monitored with video-time-depth recorders: what's missing from dive profiles?

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**ABSTRACT:** We used a turtle-mounted video and data-logging system (Cittercam; National Geographic Society, USA) to study underwater behaviour and dive patterns of green turtles, *Chelonia mydas*, at a coastal foraging area in the Gulf of California, Mexico. Between August 1997 and June 2002, units were deployed 36 times on 34 green turtles ranging from 64.1 to 96.7 cm in straight carapace length and 38.6 to 120.5 kg in weight. A total of 89.5 h of video was recorded with corresponding dive data (1065 total dives). Foraging was observed during 8 deployments (28 events) at depths of 3.0 to 32.0 m and occurred while turtles were swimming in the midwater column and stationary on the seafloor; 4 marine algae and 5 invertebrate prey species were identified. Resting behaviour was seen during 9 deployments (33 dives) as turtles set on the seafloor at depths of 7.0 to 26.5 m. Overall, 6 dive types were observed and labeled Type 1 to Type 6 dives. Green turtles foraged during Type 1, Type 3, and Type 5 dives, whereas they rested only during Type 1 dives. In addition to elucidating the importance of specific habitats and resources in neritic foraging areas, our results confirm that a variety of underwater behaviours can be reflected by 1 specific dive profile. These data indicate caution should be exercised when ascertaining in-water activity solely based on the appearance of dive profiles.

**KEY WORDS:** Behaviour · Dive type · *Chelonia mydas* · Cittercam · Habitat use · Green turtle · VTDR

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## INTRODUCTION

Two fundamental aspects of sea turtle behavioural ecology concern how individuals forage and rest within neritic habitats. Although the timing and location of these activities have been the focus of prior research, few data are available, primarily because sea turtles are difficult to observe underwater. Most studies have relied on indirect measurements via turtle-mounted electronic devices such as time–depth recorders (TDRs) and acoustic transmitters (e.g. Schmid et al. 2002, Seminoff et al. 2002a, Southwood et al. 2003). Studies utilizing these techniques often describe in-water activity subjectively according to

dive profiles and dive duration. Whereas dives of short duration and those with continuous depth fluctuations during the bottom phase are believed to represent foraging (e.g. Brill et al. 1995, van Dam & Diez 1996, Makowski et al. 2006), longer dives to a fixed depth (i.e. U-shaped dive profile) have been considered resting dives (e.g. Hochscheid et al. 1999, Hays et al. 2000, Southwood et al. 2003). These inferences suggest that dive profiles are useful for interpreting underwater activity of sea turtles in coastal foraging areas. However, the exclusive use of time–depth plots yields an empirical view of sea turtle dive behaviour, void of any information on the interaction between tracked subjects and their environment.

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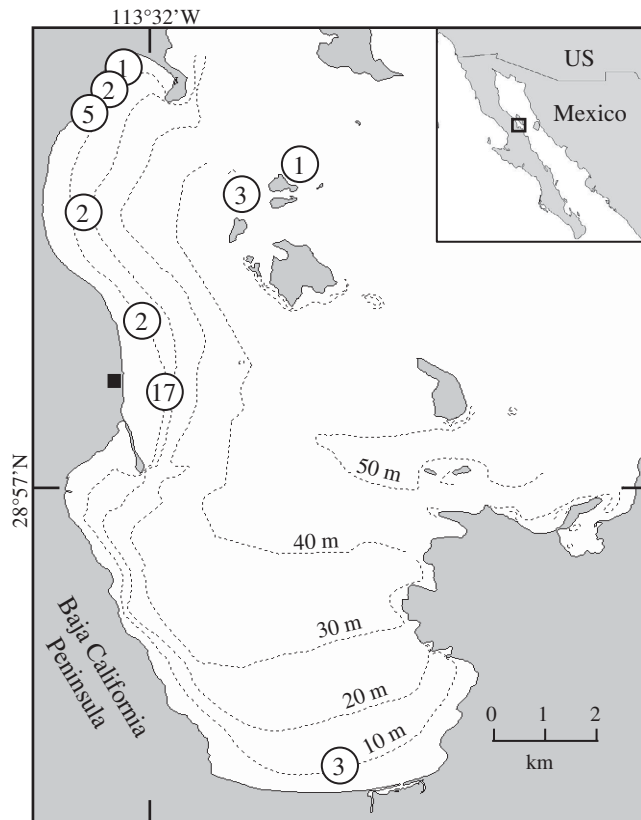


Fig. 1. Map of Bahía de los Angeles study area along the eastern coast of the Baja California Peninsula, Mexico. Circles with numbers indicate capture/release sites for Crittercam deployments. The numbers represent number of VTDR deployments at each capture/release site. Dashed lines indicate 10 m bathymetric contours. See Appendix 1 for deployment location of each individual

Over recent years, the use of animal-borne video systems that integrate TDR technology (VTDRs) has proven useful for studying the behaviours of free-swimming sea turtles (Heithaus et al. 2002b, Reina et al. 2005). In addition to producing information on a turtle's interaction with marine habitats, these systems enable researchers to link dive profiles and depths with an array of underwater activities. VTDR systems are thus able to provide insights into the variability in behaviours that are reflected by a given dive profile.

The green turtle (*Chelonia mydas*) is prime candidate for the application of VTDR technology. This species is a resident of temperate and tropical marine habitats around the world (e.g. Musick & Limpus 1997), and its coastal occupancy enables feasible deployment and recovery of VTDR systems, which must be retrieved to access collected data. Green turtles consume vast quantities of marine algae and seagrasses, and the resultant digestive processing constitutes an important conduit for energy flow in coastal

ecosystems (e.g. Thayer et al. 1982, Bjørndal 1997). Elucidating the patterns of prey acquisition and habitat use will help specify the value of marine resources for this large omnivore and will lead to greater knowledge of the structure and function of coastal marine ecosystems.

In this study, we used a turtle-mounted VTDR system (Crittercam, National Geographic Society, Washington DC) to monitor the behaviours of submerged green turtles at a temperate foraging area in the Gulf of California, Mexico. Our primary objectives were to (1) describe the foraging and resting strategies of this species through video analysis and (2) link these observations with time–depth plots to elucidate the value of dive profiles for determining underwater behaviour. This is the first study using VTDRs to monitor the behaviours of hard-shelled turtles in the eastern Pacific Ocean. When combined with conventional telemetry and dietary studies (e.g. Seminoff et al. 2002a,b), we believe the application of video technology will generate an enhanced view of green turtle ecology.

## MATERIALS AND METHODS

Between August 1997 to June 2002 we attached VTDR systems 36 times on 34 green turtles captured with entanglement nets during an ongoing study of green turtle demography at Bahía de los Angeles (28° 58' N, 113° 33' W; Fig. 1) in the Gulf of California, Mexico (Seminoff et al. 2003). Turtles selected for instrumentation were captured among 9 sites throughout the study area (Fig. 1), and they ranged from 64.1 to 96.7 cm (mean =  $79.6 \pm 1.5$  cm) in straight carapace length (SCL) and from 38.6 to 120.5 kg (mean =  $75.1 \pm 4.1$  kg) in body weight (Appendix 1). Although 2 turtles were missing large portions of a front flipper, all turtles otherwise appeared to be in fine health. VTDR-fitted turtles were released at their site of initial capture within 24 h.

**VTDR technology.** The VTDR system consisted of a Hi-8 video camera integrated with a time–depth recorder and on-board microcomputer (512 kb of memory). These components were packaged in a cylindrical aluminum housing (diameter: 10.1 cm; length: 31.7 cm) that had a hydrodynamically optimized dome and conical tail portion composed of incompressible syntactic foam (Fig. 2). Five different units were used during this study. For recovery, these units were equipped with a very-high-frequency (VHF) radio transmitter (MOD 050, Telonics, Mesa, AZ, USA) and acoustic (ultrasonic) tag (CHP-87-L, Sonotronics, Tucson, AZ). VTDRs weighed 2 kg out of the water (1.7 to 5.2% of turtle body weight), but were slightly posi-



Fig. 2. *Chelonia mydas*. Green turtle (BLA 511) in Bahía de los Angeles equipped with a VTDR (Critttercam, National Geographic Society, Washington, DC). Whereas this turtle was 68.1 cm SCL, the size range of all turtles examined during this study was 64.1 to 96.7 cm SCL

tively buoyant in water; however, this buoyancy was rendered neutral during deployments due to the attachment of counterweights on the attachment base plate (see below). We programmed VTDRs to collect audio and video in both short-play (3 h) and long-play (6 h) modes and to record continuously or at a 5 min on/5 min off duty cycle. Pressure (i.e. water depth) data were collected at a range of intervals between 2 to 7 s. Depth measurement resolution and maximum depth were 0.5 and 500 m, respectively. The units were calibrated in a standard pressure facility at the National Geographic Society Remote Imaging Laboratory, Washington, DC, USA.

We attached VTDRs to the crown of each turtle's carapace with a 2-plate mechanism: the top plate was connected to the housing with 2 hose clamps; the bottom plate was fitted with a nylon-mesh apron, and attached to the carapace with 5 min quick-set epoxy. The front of these plates was connected by an interlocking assembly, and the back was linked with a burn-wire connector and backup corrosive (Mg) link. VTDRs were programmed to detach 3 to 20 h after deployment, at which time a charge from an on-board 9V battery was sent to the burn-wire, causing the wire to corrode and break, thereby disengaging the plates. Once detached from the counterweighted baseplate, the slight positive buoyancy of the VTDR brought it to the surface. For 11 of the 36 deployments, we tracked turtles for the entire deployment duration following protocol described in Seminoff et al. (2002a). Surfacing positions and times were recorded for calculation of swim speed and total distance traveled.

**Video and data analysis.** Video images were copied from Hi-8 format to VHS format, then time-stamped

and viewed using a standard VCR. We described 4 primary classes of turtle activity: surfacing, travelling, foraging, and resting. Surfacing events were coded when a turtle's head broke the surface of the water and included activity while the water's surface could be seen in the video. Travelling was recorded for turtles undertaking 'midwater' dives with no visits to benthic substrata. Foraging was inferred when (1) a specific food item was seen ingested by a turtle, (2) an item in the video went out of view and was followed immediately by chewing motions, often accompanied by sound of mastication, or (3) fragments of a prey item were seen expelled through the external nares of the turtle. All ingested items that could be seen were identified to the lowest taxon. Handling times for each food item were calculated as the interval from when a turtle engaged with a prey item to when all apparent food intake (i.e. mastication) ceased. We determined the depth of each foraging event and summarized foraging depth as the number of events in each of five 10 m depth categories (0 to 50 m) that reflect the depths within the study area. A turtle was coded as resting when it appeared motionless with no apparent head or flipper movements.

Depth data were graphed using the program Lite-Show (Onset Computers, Bourne, MA, USA). All vertical movements to  $\geq 1.5$  m depth were considered dives. We characterized each dive visually by the general shapes of descent, bottom, and ascent phases of time-depth plots. We also calculated depth (m) and duration (min) for each dive. Depth was defined as the deepest point on the dive profile. To determine dive duration, we defined the beginning and end of dives as the first of 3 successive data samples of increasing depth to below 1.5 m and the last of a set of 3 ascending data points of decreasing depth to above 1.5 m, respectively. We used linear regression to examine the relationships of mean depth versus mean duration among turtles for each dive type, as well as turtle size (log weight) versus dive depth and dive duration. Analyses of variance (ANOVA) were used to compare dive type with mean depth and mean duration among turtles, and to compare depths of dives containing foraging and resting. For turtles that exhibited continuous resting dives, we used the mean depth and mean duration of the respective continuous dive sequence for the analyses. A Tukey-Kramer HSD post-hoc test was used to determine significant differences among mean depths and durations for each dive type. Only dives with concurrent video were included in analyses. Although it is common practice to exclude the early portions of dive and video data subsequent to deployment, we analyzed all data since several behaviours were observed during the earliest portions of each deployment. Statistical analysis was performed with

Table 1. Summary of dive data for 25 video-time-depth recorder deployments on green turtles in Bahía de los Angeles. Only dive data for which concurrent video was collected are given. Analyses are based on means from each deployment. Results of the Tukey HSD test: means having at least 1 superscript in common are not significantly different

Dive characteristics	Dive type:	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
No. of deployments		19	26	12	17	22	9
No. of dives with video		71	561	52	109	234	38
Mean dive depth (m)		20.0 ± 3.3 <sup>a</sup>	14.1 ± 2.3 <sup>b</sup>	10.3 ± 1.7 <sup>b</sup>	13.7 ± 2.9 <sup>b</sup>	7.0 ± 1.3 <sup>b</sup>	18.5 ± 2.8 <sup>a</sup>
Mean dive depth range (m)		7.0–47.8	3.3–41.5	3.5–25.9	5.1–26.6	3.1–17.6	4.7–31.8
Mean dive duration (min)		12.6 ± 1.4 <sup>a</sup>	4.3 ± 0.7 <sup>b</sup>	8.2 ± 1.6 <sup>a,b</sup>	10.0 ± 2.4 <sup>a</sup>	4.5 ± 0.8 <sup>b</sup>	9.5 ± 5.3 <sup>a</sup>
Mean dive duration range (min)		7.0–26.1	1.6–16.0	3.0–25.3	4.0–28.1	2.0–11.3	3.4–21.0
Depth (x) vs duration (y)		$y = 0.22x + 8.11$	$y = 0.27x + 1.11$	$y = 0.70x + 2.45$	$y = 0.69x + 2.35$	$y = 0.56x + 1.44$	$y = 0.42x + 3.35$
Regression statistics		$F_{1,18} = 4.23$ $R^2 = 0.28$ $p = 0.06$	$F_{1,25} = 52.39$ $R^2 = 0.72$ $p < 0.001$	$F_{1,11} = 14.29$ $R^2 = 0.54$ $p = 0.003$	$F_{1,16} = 16.36$ $R^2 = 0.67$ $p = 0.004$	$F_{1,21} = 48.29$ $R^2 = 0.81$ $p < 0.001$	$F_{1,8} = 32.84$ $R^2 = 0.73$ $p < 0.001$
Observed foraging activity		Yes	No	Yes	No	Yes	No
Observed resting activity		Yes	No	No	No	No	No

JMP software (SAS Institute 1996). Values for significance were set at  $p < 0.05$ . Mean values are given ± standard error (SE).

## RESULTS

### Deployment and tracking summary

The deployment durations of VTDRs ranged from 0.3 to 20.0 h (mean =  $4.6 \pm 0.74$  h). Video and dive data were successfully recorded during 30 deployments and 27 deployments, respectively. On several deployments, camera and/or electrical malfunctions prevented data collection or caused premature detachment (Appendix 1). VTDR deployments occurred primarily during daylight periods (06:00 to 19:30 h) with 98.3% of video and 93.5% of dive data collected during this interval. Among the deployments during which turtles were tracked continuously ( $n = 11$ ), track lengths ranged from 2.6 to 12.7 km (mean =  $5.6 \pm 1.0$  km), resulting in mean swimming speeds of 0.9 to  $2.0 \text{ km h}^{-1}$  (overall mean =  $1.4 \pm 0.1 \text{ km h}^{-1}$ ).

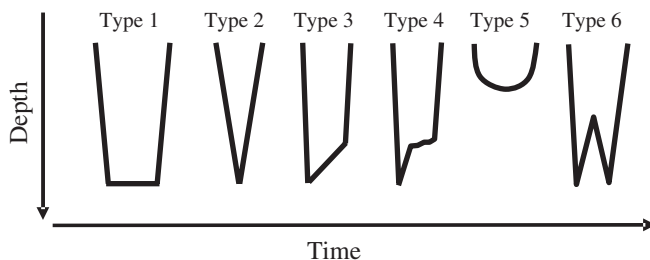


Fig. 3. Generalized profiles for the 6 dive types undertaken by green turtles

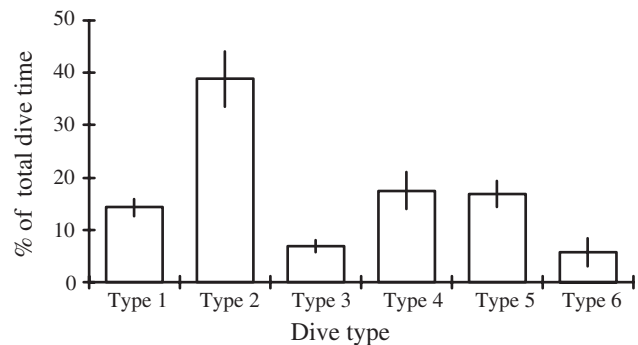


Fig. 4. Proportion of total dive time for each dive type

### Dive patterns

A total of 1065 dives (93.8% of all dives) had corresponding video (Table 1). Green turtles conducted from 6 to 128 dives per deployment. We observed 6 different dive types; a generalized profile for each type is presented in Fig. 3. To maintain consistency with previous sea turtle diving studies, we labeled dives following terminology from Minamikawa et al. (1997) and Houghton et al. (2002). These included Type 1, Type 2, Type 3, Type 4, and Type 5. We also observed a sixth dive type (Type 6) that, although shown graphically (Southwood et al. 2003, Reina et al. 2005), has not been labeled previously. Type 6 dives were W-shaped, with the initial descent followed by an ascent of  $\geq 2$  m, then a second descent of  $\geq 2$  m before the final ascent to the surface. This dive profile reflected midwater dives ( $n = 27$ ) and dives to the seafloor ( $n = 11$ ).

Table 1 summarizes the frequency, depth, duration, and turtle activities for each dive type. Type 2 dives comprised the greatest proportion of total dive time,



whereas Type 3 and Type 6 dives constituted the smallest proportions of total dive time (Fig. 4). Maximum dive depth and dive duration for each deployment ranged from 11.0 to 54.5 m (mean =  $28.4 \pm 2.1$  m) and from 5 to 48 min (mean =  $16.1 \pm 1.7$  min), respectively; there was no significant relationship between turtle weight and maximum dive depth ( $p = 0.86$ ) or maximum dive duration ( $p = 0.36$ ). The relationships between mean dive depth and mean dive duration were significant for all dive types except Type 1 dives, although the latter was only marginally non-significant ( $p = 0.06$ , Table 1). Among dive types, there were significant differences in mean dive depths ( $F_{1,5} = 3.54$ ,  $p = 0.006$ ) and mean dive durations ( $F_{1,5} = 6.40$ ,  $p < 0.001$ ). Type 1 and Type 6 dives were significantly deeper than Type 5 dives; and Type 1, Type 4, and Type 6 dives were significantly longer than Type 2 and Type 5 dives (Tukey HSD,  $p \leq 0.05$ ).

### Linking video with dive data

A total of 89.5 h of video (86.4 % of all video) had corresponding dive data. The most common activities observed in the video were surfacing and travelling movements. During travelling, the video often depicted the turtle's fully extended neck and head bobbing in conjunction with flipper strokes (Fig. 5a); green turtles would occasionally move their head from side to side in apparent attempts to survey the water column. Amidst travelling dives, green turtles would occasionally undertake exploratory Type 2 dives to the seafloor to survey benthic habitats (Fig. 6a).

Twenty-eight feeding events were observed on video among 8 deployments. Prey handling times ranged from 0.1 to 6.9 min overall, resulting in 51.4 min of foraging activity among all deployments (Table 2). From 0 to 16 foraging events occurred in each 10 m depth class. The greatest proportion of feeding occurred in the 0 to 9.9 m depth class, with a lesser peak in the 20.0 to 29.9 m depth class (Fig. 7). The initial feeding bouts during each deployment occurred 6.2 min to 10.7 h after release. Low-light conditions and/or turtle-head silhouettes obscured the view on 7 feeding events. Of the prey items that were clearly seen, 4 marine algae species and 5 invertebrates were identified (Table 2).

We observed 3 foraging strategies: stationary foraging ( $n = 22$  events), active benthic foraging ( $n = 4$  events), and active midwater foraging ( $n = 2$  events). Stationary foraging occurred at depths of 3.5 to 32.0 m as turtles sat on the seafloor during Type 1 dives. This foraging strategy was associated with algae pastures, mixed algae/gorgonian (Gorgoniidae) fields, black coral (*Antilopathes galapagensis*) patches, and deep-

water anoxic substrate zones. The latter habitat hosted a previously undescribed stationary foraging tactic: during 7 Type 1 dives to greater than 25 m, green turtles were seen making head lunges into anoxic small-particle substrate, expelling silt-laden water through their nostrils while showing head movements consistent with mastication (Fig. 6b see video at: [www.int-res.com/articles/suppl/m322p269\\_videos/](http://www.int-res.com/articles/suppl/m322p269_videos/)). Solitary tube worms (*Bispira* sp.) were the confirmed prey species during 2 of these 'benthic sifting' events. Other foods consumed during stationary foraging included marine algae (Rhodophyta and Chlorophyta; Table 2, Fig. 5c,d), and black coral polyps (Table 2). Active benthic foraging occurred during Type 1 dives as turtles moved along sandy benthic substrates at depths of 4.5 to 27.0 m. The foods consumed during these active benthic foraging events included sea pens (*Ptilosarcus undulatus*; Table 2, Fig. 5e,f) and algae fragments. Active midwater foraging targeted prey in the water column and occurred during the initial ascent of a Type 3 dive at a depth of 8.0 m (consumption of *Sargassum* sp.; Table 2, Figs 5b & 6c) and during the ascent of a Type 5 dive at a depth of 5.0 m (consumption of a Scyphozoan; Table 2, Fig. 6d).

We recorded 33 resting dives that ranged from 12.5 to 26.0 m in depth. Green turtles ranging from 38.6 to 85.9 kg were observed resting, but the relationship between turtle weight and resting dive duration was not significant ( $p = 0.83$ ), nor was the relationship between turtle weight and resting dive depth ( $p = 0.67$ ). Resting occurred during periods that encompassed  $\geq 2$  sequential Type 1 dives ('continuous resting';  $n = 2$  to 14 dives per resting sequence, 4 deployments; Fig. 6e) and during single Type 1 dives ('episodic resting';  $n = 9$  deployments; Fig. 6f). Continuous resting dives occurred during early afternoon (13:00 to 15:00 h,  $n = 16$  dives), late afternoon (17:30 to 19:00 h,  $n = 3$  dives), and nocturnal periods (22:30 to 05:00,  $n = 3$  dives). These dives ranged from 4.2 to 23.6 min (mean =  $13.1 \pm 2.8$  min) in duration and occurred as turtles sat motionless on the seafloor within patches of black coral ( $n = 17$  dives), marine algae pastures dominated by *Padina durvillaei* ( $n = 3$  dives; Fig. 5g), and insular boulder habitats ( $n = 2$  dives). All episodic resting dives occurred during early afternoon (13:00 to 15:00 h) and ranged from 1.8 to 22.5 min in duration (mean =  $11.9 \pm 1.1$  min). During episodic resting, turtles sat on the sea floor within black coral patches ( $n = 7$  dives; Fig. 5h) and boulder habitats ( $n = 4$  dives). Overall, green turtles rested for 130.9 min during episodic resting dives, and 288.2 min during continuous resting dives. No turtle was seen wedging itself within vertical features and no turtle was observed resting in the midwater column amidst dives.

Type 1 dives had the greatest number of associated

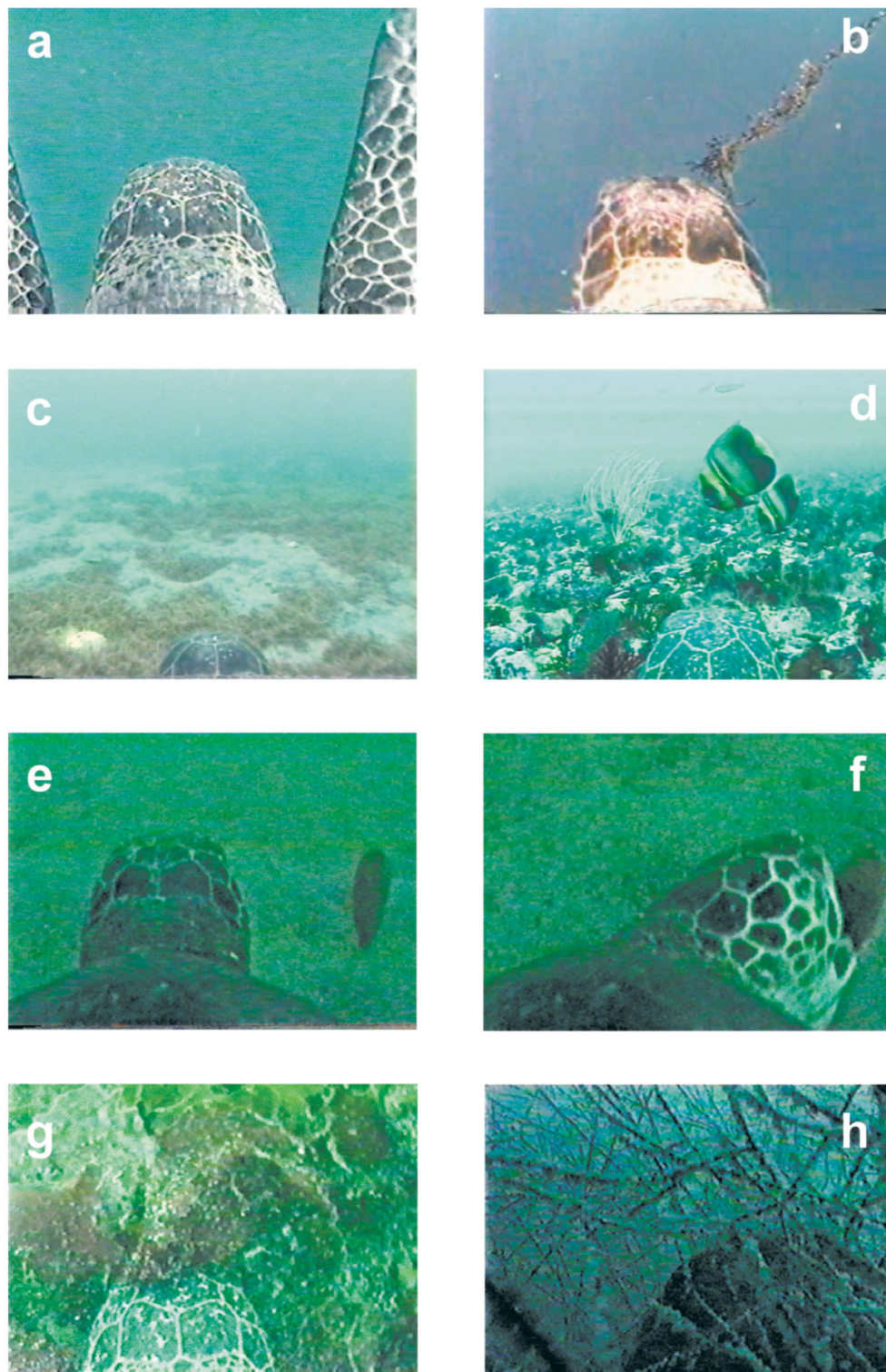


Fig. 5. *Chelonia mydas*. Video frames collected by Crittercam: (a) traveling movements, CM-4; (b) active midwater foraging on *Sargassum* sp., CM-24; (c) stationary benthic foraging at *Gracilariopsis* pasture, CM-26; (d) stationary benthic foraging at mixed algae/gorgonian pasture, CM-14; (e,f) active benthic foraging on sea pen *Ptilosarcus undulatus*, CM-20 (images recorded 3 s apart); (g) continuous resting in *Padina durvillaei* pasture, CM-4; (h) episodic resting in a patch of black coral *Antipathes galapagensis*, CM-5. Video clips from which each image was taken, as well as additional clips, are available at: [www.int-res.com/articles/suppl/m322p269\\_videos/](http://www.int-res.com/articles/suppl/m322p269_videos/)

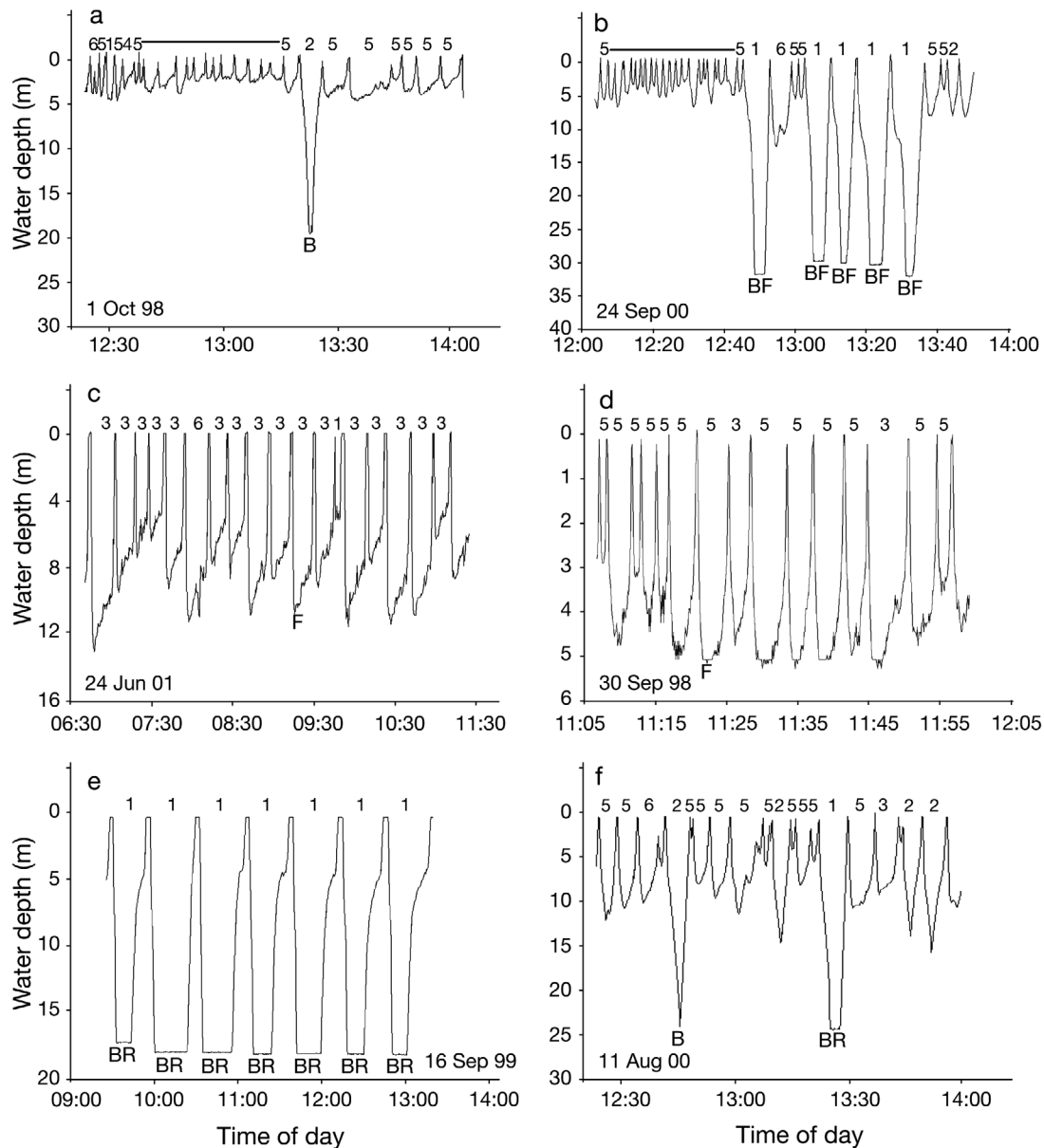


Fig. 6. Examples of dive-profile sequences that had corresponding video footage: (a) exploratory Type 2 dive (to ca. 20 m) amidst shallow dives; (b) Type 1 dives (to ca. 30 m) with benthic foraging amidst shallow dives; (c) Type 3 dives with midwater foraging event; (d) Type 5 dives with midwater foraging event; (e) continuous resting Type 1 dives, (f) variable dives with a benthic exploratory Type 2 dive and an episodic resting Type 1 dive. Numerals above each dive profile indicate the dive type; letters below dive profiles indicate underwater activity: *B* = benthic dive, *F* = foraging, *R* = resting

underwater activities of all dive types. Of the 71 Type 1 dives with corresponding video, 11 were episodic resting dives, 22 were part of continuous resting sequences, 25 included horizontal movements along the seafloor without foraging, and 13 contained foraging (Table 3). Among these 4 activity classes there was no evidence of a difference in dive depths ( $F_{3,51} = 0.96$ ,  $p = 0.42$ ) but there was a difference in dive durations ( $F_{3,51} = 7.06$ ,  $p < 0.001$ ). Continuous and episodic resting Type 1 dives were significantly longer than both

movement and foraging Type 1 dives; foraging Type 1 dives were significantly shorter than all other Type 1 dives (Tukey HSD,  $p \leq 0.05$ ).

## DISCUSSION

Despite the increasingly widespread application of telemetry techniques to study sea turtle activity, published information on the behavioural patterns and habi-



Table 2. Diet items seen on video during VTDR deployments. If prey item was consumed on more than 1 occasion, depth and handling time ( $T_h$ ) are given as ranges. B = benthic foraging; M = foraging in the midwater column

Prey item	Common name	Depth (m)	Location	$T_h$ (min:s)	No. of events
Chlorophyta					
<i>Ulva lactuca</i>	Sea lettuce	4.5	B	01:20	1
Phaeophyta					
<i>Sargassum johnstonii</i>	Sargassum	3.0	M	00:23	1
Rhodophyta					
<i>Gracilariopsis lemaneiformis</i>	Red algae	8.0	B	00:34–06:01	2
<i>Gigartina</i> sp.	Red algae	7.5–9.0	B	04:22–06:54	3
Unidentified marine alga	Algae	4.5–17.0	B	00:08–00:30	5
Cnidaria					
Scyphozoa (Medusa)	Sea jelly	5.5	M	00:03	1
<i>Ptilosarcus undulatus</i>	Fleshy sea pen	27.0	B	00:05	1
<i>Antipathes galapagensis</i>	Yellow-polyp black coral	18.0–23.5	B	02:10–05:36	3
<i>Lytocarpus nuttingi</i>	Hydroid	24.5	B	00:50	1
Annelida					
<i>Bispira</i> sp.	Fanworm	5.5–32.0	B	00:07–01:21	3
Unidentified		4.5–32.0	B	00:03–02:24	7

tat use of free-ranging sea turtles is scarce. The present VTDR application represents one of the few studies of sea turtles employing this technology (see also Heithaus et al. 2002b, Reina et al. 2005). Overall we were successful in describing 6 general dive patterns (i.e. Type 1 to Type 6 dives) and 8 underwater behaviours: (1) midwater travelling, (2) benthic exploration, (3) horizontal movements along the seafloor, (4) active midwater foraging, (5) active benthic foraging, (6) stationary benthic foraging, (7) continuous resting, and (8) episodic resting. Green turtles engaged in these behaviours while interacting with 7 habitat types. Linking these data has elucidated ecological aspects of green turtles at a warm temperate foraging area and has contributed to our general knowledge about the variability of green turtle behaviours during submergence.

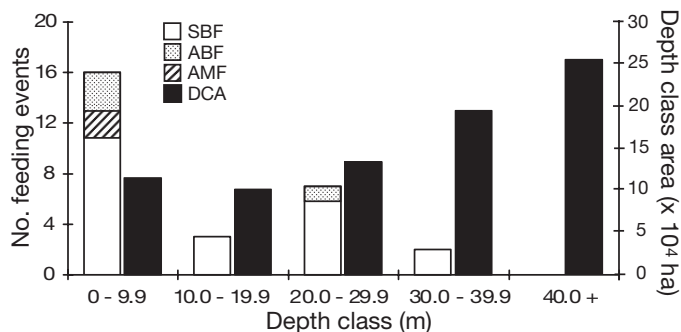


Fig. 7. Frequency of foraging events summarized by 10 m depth classes. SBF: stationary benthic foraging; ABF: active benthic foraging; AMF: active midwater foraging. Prey species were identified during 21 of the 28 feeding events (see Table 4). DCA: corresponding area (ha) of depth class within Bahía de los Angeles

### Dive profiles versus underwater activity

The dive profiles exhibited by green turtles were consistent with those previously reported for hard-shelled sea turtles, although we found a greater diversity of behaviours during the respective dive types. For example, whereas Type 1 dives are often attributed to resting (e.g. van Dam & Diez 1996, Hays et al. 2000, Southwood et al. 2003), we also observed active and stationary benthic feeding as well as horizontal movements in video from these dives. Variation in dive activity was also seen during Type 2, Type 3, Type 5, and Type 6 dives, all of which have commonly been linked to orientation and travelling movements (e.g. Hochscheid et al. 1999, Hays et al. 2001, Houghton et al. 2002). In addition to the travelling, green turtles were observed visiting benthic habitats during apparent exploratory behaviour during Type 2 and Type 6 dives, and they were seen actively foraging in the midwater column during Type 3 and Type 5 dives. The potential for multiple behaviours to be reflected by a single dive profile type has been suggested elsewhere (van Dam & Diez 1996, Minamikawa et al. 1997, Hochscheid & Wilson 1999, Hochscheid et al. 1999), but few data are available due to the paucity of direct field observations. In the Mediterranean Sea, Houghton et al. (2000) observed loggerhead turtles (*Caretta caretta*) consuming mollusks in benthic habitats during dives that would be interpreted as resting dives. Heithaus et al. (2002b) used VTDRs to show that Australia green turtles exhibit a novel rubbing behaviour on sponge outcrops during dives that would normally be considered foraging dives. Coupled with these find-



ings, our results indicate that caution should be used when ascertaining the function of individual dives based solely upon their time–depth plots.

### Foraging strategies

By revealing novel diet items and elucidating the strategies undertaken by green turtles to consume prey, VTDR systems complement conventional diet study techniques such as esophageal lavage and fecal analysis. The consumption of 9 different prey species was seen in the video, including two (*Sargassum* sp. and annelid worms) that were previously described as incidental diet items (Seminoff et al. 2002b; Table 2). Also included in this group was a Scyphozoan, the first gelatinous prey described for green turtles in the region despite extensive dietary research (Seminoff et al. 2002b, unpubl. data). To our knowledge, the only other report of Scyphozoan consumption by green turtles in neritic habitats was also gathered via VTDR data (Heithaus et al. 2002b). Perhaps the large size and/or rapid digestion of gelatinous prey inhibit recovery via conventional dietary analyses. If so, animal-borne imagery may be the best tool for revealing consumption of such items. However, we acknowledge that, while VTDR systems may be superior for determining the presence of diet items and their mode of intake (i.e. directed versus incidental), other techniques such as stable isotope analysis (Godley et al. 1998) and fatty-acid analysis (Seaborn et al. 2005) are more effective for determining the relative energetic importance of ingested foods.

Through deployment of VTDRs, we learned that green turtles engage in stationary and active benthic foraging at depths of 3.0 to 32.5 m, and they actively forage in the midwater column at depths of 3.0 and 5.0 m (Table 2, Fig. 7). Stationary foraging by green turtles over nearshore algae pastures has been reported at other sites (e.g. Bjørndal 1997), but no studies have

described this foraging tactic in deeper waters away from herbivorous food patches. The offshore benthic foraging peak at 20.0 to 29.9 m (Fig. 7) is likely tied to the distribution of the yellow-polyp black coral fields that start at ca. 17 m depth (J. Seminoff pers. obs.). However, the benthic sifting of small-particle anoxic substrate at depths >30 m indicates that green turtles access even deeper sites on occasion. Although some offshore foraging, particularly in the midwater column, may be an opportunistic response to prey availability, this is clearly not always the case, as indicated by the repeated visits to these sites (e.g. Fig. 6d). Nevertheless, foraging was infrequent in the deepest portions of the study area (Fig. 7), thus providing further evidence that shallow zones provide the most important foraging habitat for green turtles.

### Resting behaviour

Continuous resting sequences have been reported in numerous earlier studies (eg. van Dam & Diez 1996, Hays et al. 2000, Makowski et al. 2006), but our study is the first to show episodic resting dives by sea turtles. Assuming that dive duration is inversely related to metabolic activity (Prange 1976), the longer duration of episodic resting dives versus foraging and movement Type 1 dives indicates that green turtle metabolic rates slowed somewhat. There was little variation between mean episodic resting dive durations (11.9 min) and continuous resting dive durations (13.1 min), and the mean depth of these resting strategies was almost identical (20.9 m and 20.2 m, respectively; Table 3). Therefore, episodic resting may afford the same per-dive energetic savings as continuous resting. These parallels, coupled with the similarity in habitats visited during episodic and continuous resting, also suggest that turtles engaging in resting behaviour seek similar shelter sites, regardless of the resting duration.

Resting in close association with marine algae pastures, black coral patches and boulder fields indicates that vertical features are a key component of resting microsites for green turtles in Bahía de los Angeles. We believe there are at least 2 possible explanations for this. First, the location of resting may be an attempt to avoid strong currents, which could negatively affect the turtle's ability to remain motionless and conserve energy: Bahía de los Angeles has a vertical tidal flux of >2 m and lateral current flow in excess of 12 km h<sup>-1</sup> (Bray & Robles 1991; J. Seminoff unpubl. data). Second, by diving to

Table 3. Summary of dive depth and duration for Type 1 dives with corresponding video summarized by dive function. 'Movement' indicates movements at maximum depth but no foraging. Continuous resting dive values were calculated with the mean depth and duration of all dives in each respective continuous dive sequence (22 dives among 4 deployments). Results of the Tukey HSD test: means having at least 1 superscript in common are not significantly different

Type 1 dive activity	Type 1 dive count	Dive depth (m)		Dive duration (min)	
		Mean ( $\pm$ SE)	Range	Mean ( $\pm$ SE)	Range
Movement	25	24.1 $\pm$ 1.9 <sup>a</sup>	3.0–43.5	7.6 $\pm$ 1.7 <sup>a</sup>	2.0–32.0
Foraging	13	18.6 $\pm$ 2.8 <sup>a</sup>	4.5–32.5	3.8 $\pm$ 1.6 <sup>b</sup>	1.4–7.1
Episodic resting	11	20.9 $\pm$ 3.0 <sup>a</sup>	12.5–26.0	11.9 $\pm$ 1.0 <sup>c</sup>	1.8–22.5
Continuous resting	22	20.2 $\pm$ 5.0 <sup>a</sup>	13.5–26.0	13.1 $\pm$ 2.8 <sup>c</sup>	4.2–23.6

the seafloor and resting near vertical features, green turtles presumably minimize their susceptibility to predation. Sharks are the primary predator of sea turtles (e.g. Heithaus et al. 2002a), and observations of missing flippers and bite marks on green turtles captured locally indicate shark predation in the region (Seminoff et al. 2003).

Although green turtles show affinity to vertical features during resting in benthic habitats, they were never observed to wedge between boulders or below overhanging ledges, thus indicating that either neutral or negative buoyancy was achieved. However, assuming that the relationship between turtle size and lung volume is relatively constant among disparate green turtle populations, the relatively small size of green turtles examined in this study suggests that green turtles exceeded the maximum depths at which neutral buoyancy could be achieved. Whereas Hays et al. (2000) hypothesized that green turtles at Ascension Island (109.0 to 127.7 cm curved carapace length [CCL]) maintain neutral buoyancy at depths no greater than 19.0 m, the green turtles in this study rested at depths of up to 26.0 m despite substantially smaller size (range = ~68.7 to 102.5 cm CCL based on the conversion  $CCL = (1.0363 \times SCL) + 2.2464$ ; Seminoff et al. 2003). Although we cannot rule out the possibility that the VTDR affected resting depths in some way, the deeper depths observed in this study suggest that buoyancy control may not be a universal strategy employed by resting green turtles. The lack of a correlation between turtle size and resting depth found in this study supports this theory, and it suggests that resting depth by green turtles is a result of active habitat selection rather than a consequence of lung volume.

#### Does the Crittercam record natural behaviours?

Because instrumented turtles were studied for the purpose of extrapolation to untagged individuals, it is important to consider the extent to which results are biased by the effects of the Crittercam system. Although there is a possibility that some underwater behaviours were altered due to the presence of the relatively large instrument, we tried to minimize such effects by designing the housing with the most hydrodynamically efficient shape possible, and by counter-weighting the attachment base plate to create a neutrally buoyant unit. The negligible nature of the Crittercam's impacts on green turtle underwater activities was evidenced by the following facts: (1) a comparison demonstrated that the mean swim speeds of the 11 tracked turtles were consistent with those from 8 turtles of similar size tracked in the study area with ultrasonic telemetry (2-sample *t*-test,  $p = 0.94$ ; J. Seminoff unpubl. data); (2) the

dive profiles and depths achieved during dives were consistent with previous studies of green turtle dive behaviour (J. Seminoff unpubl. data); and (3) normal daily activities such as foraging and resting were exhibited by green turtles within minutes of release. In addition, previous studies employing the Crittercam have also shown negligible effects of the units on behaviour. Parrish et al. (2000) found that Hawaiian monk seals foraged and dived normally with a Crittercam attached for up to 3 d. Heithaus et al. (2001) reported that Crittercam-equipped tiger sharks (*Galeocerdo cuvier*), showed no abnormal behaviour with respect to habitat selection, foraging behaviour or swim speed.

## CONCLUSIONS

Our results include 2 important findings that bear on the study of underwater activity by sea turtles. First, the integration of time–depth plots with video indicates that a single dive profile may reflect more than one behaviour. This variability suggests that caution should be exercised when ascertaining activity solely based on dive patterns. Second, the observation that green turtles feed and rest at variable depths and in multiple habitats indicates that the empirical view afforded by exclusive use of time–depth plots is insufficient for determining the interactions of sea turtles with benthic substrates, particularly in areas with a complex habitat mosaic. This underscores the value of image data for depicting the interactions of turtles with diverse habitats. Although these are helpful advances, it is important to note that our results are heavily biased toward daytime activity (98% of all video) of larger turtles (mean =  $75.1 \pm 4.1$  kg), the result of the VTDR's inability to monitor during low-light conditions and its relatively large size. To facilitate broader studies, we encourage the wider application of night-vision VTDR systems as well as the continued miniaturization of these and other animal-borne electronic devices. The use of other tools, such as flipper-beat sensors (Hays et al. 2004), beak-movement sensors (Hochscheid et al. 2005), and stomach-temperature transmitters (Andrews 1998), will also further elucidate the behaviours of sea turtles in marine habitats.

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Appendix 1. Summary of VTDR deployments on green turtles in Bahía de los Angeles between August 1997 and June 2002. SCL = straight carapace length (cm). (•) Successful collection of dive data and video. See Fig. 1 for location of initial release site of each deployment

Deployment number	Date	Site	Turtle ID	SCL (cm)	Weight (kg)	Dive data	Video
CM-01	15 Aug 1997	9	BLA 219	77.3	67.3		
CM-02	19 Aug 1997	5	BLA 220	70.1	61.4	•	•
CM-03	24 Sep 1998	6	BLA 339	80.2	81.8	•	
CM-04	26 Sep 1998	3	BLA 231 <sup>a</sup>	94.7	111.8	•	•
CM-05	28 Sep 1998	3	BLA 340	74.0	54.1	•	•
CM-06	30 Sep 1998	6	BLA 342	90.7	108.6	•	•
CM-07	30 Sep 1998	6	BLA 224	74.6	53.2	•	•
CM-08	01 Oct 1998	6	BLA 343	85.1	84.5	•	•
CM-09	13 Sep 1999	6	BLA 137	89.4	101.8		
CM-10	14 Sep 1999	6	BLA 434	80.2	70.9		
CM-11	15 Sep 1999	6	BLA 433	73.8	59.1	•	
CM-12	16 Sep 1999	6	BLA 432	64.1	38.6	•	•
CM-13	18 Sep 1999	1	BLA 422 <sup>a</sup>	66.6	47.7	•	
CM-14	19 Sep 1999	6	BLA 425	81.4	77.3	•	•
CM-15	21 Sep 1999	6	BLA 438	78.9	64.5	•	•
CM-16	22 Sep 1999	6	BLA 329	89.0	90.5	•	•
CM-17	28 Jun 2000	6	BLA 426	88.7	111.4	•	
CM-18	29 Jun 2000	6	BLA 511	68.1	40.9		
CM-19	02 Jul 2000	6	BLA 512	85.6	73.2	•	
CM-20	11 Jul 2000	4	BLA 515	77.5	54.5	•	•
CM-21	18 Jul 2000	6	BLA 516	77.5	68.2	•	•
CM-22	24 Jul 2000	6	BLA 518	70.5	49.5	•	•
CM-23	28 Jul 2000	2	BLA 231 <sup>a</sup>	96.7	119.1	•	•
CM-24	26 Jul 2000	4	BLA 406	85.7	85.9	•	•
CM-25	02 Aug 2000	5	BLA 519	81.4	79.5	•	•
CM-26	11 Aug 2000	6	BLA 520	82.1	75.0	•	•
CM-27	13 Aug 2000	3	BLA 521	71.6	56.8	•	•
CM-28	15 Aug 2000	2	BLA 422 <sup>a</sup>	68.4	50.0	•	•
CM-29	16 Aug 2000	3	BLA 522	64.9	38.6	•	•
CM-30	17 Aug 2000	8	BLA 523	88.0	107.7	•	•
CM-31	18 Aug 2000	8	BLA 525	95.7	120.5	•	•
CM-32	23 Aug 2000	8	BLA 524	70.2	45.9	•	•
CM-33	24 Jul 2001	7	BLA 614	82.0	72.3	•	
CM-34	01 Aug 2001	7	BLA 430	71.0	64.8	•	•
CM-35	03 Aug 2001	3	BLA 601	86.1	115.5	•	•
CM-36	20 Jun 2002	7	BLA 706	83.5	115.5	•	

<sup>a</sup>Turtle was studied on 2 occasions

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